First Virginia Records of Four European Insect Herbivores of *Phragmites australis*

Bernd Blossey

Department of Natural Resources Fernow Hall, Cornell University Ithaca, New York 14853

Joseph T. Weber

Division of Natural Heritage Virginia Department of Conservation and Recreation 217 Governor Street Richmond, Virginia 23219

INTRODUCTION

Common reed, Phragmites australis (Cav.) Trin. ex Steudel, is a clonal cosmopolitan grass species with rapidly expanding populations in both freshwater and brackish North American wetlands, particularly along the Atlantic Coast (Marks et al., 1994). Recruitment from seed is generally low, and vegetative propagation and clonal expansion occur through dispersal of rhizome fragments. The extensive belowground rhizome system produces homogenous stands with up to 200 stems/m² that can reach 4 m in height (Haslam, 1972). Low nitrogen or phosphorous availability, high salinity, extensive tidal flooding, and anaerobic soils may limit the expansion of P. australis clones (Chambers, 1997). The rapid expansion of P. australis in North America during the past several decades has resulted in the replacement of mixed wetland plant communities by monotypic P. australis stands, causing detrimental impacts on native wildlife (Marks et al., 1994). This invasion is considered a threat to biodiversity in natural areas and has resulted in aggressive control attempts (Marks et al., 1994). Recommendations for P. australis control include the use of herbicides, mowing, disking, dredging, flooding, draining, burning, mulching, and grazing. Currently, the most widespread and successful approach appears to be the application of glyphosate late in the growing season, followed by prescribed burning or mechanical removal of dead stalks, and subsequent application of glyphosate the next year. In order to maintain areas with low *P. australis* abundance, however, retreatments are usually necessary every 3-5 years and negative side effects on non-target plants are inevitable if non-selective herbicides are used over large areas. At present, there is no long-term, species-specific control measure.

The commitment of wetland managers to reduce P. australis populations in North America has increased interest in alternatives to currently used control techniques. One alternative to chemical, mechanical, and physical control is biological control, the introduction of host-specific natural enemies (usually insects, less often pathogens) from the native range of an introduced plant (Tewksbury et al., in prep.). The status of P. australis as native or introduced is not resolved, and it has been hypothesized that a more aggressive genotype of European origin has been introduced (Metzler & Rosza 1987; Tucker, 1990; Mikkola & Lafontaine, 1994; Besitka, 1996). This hypothesis is being evaluated using advanced genetic techniques (K. Saltonstall, pers. comm.). Regardless of its status as native, introduced, or both, control attempts continue. As part of an evaluation of the potential of developing biological control of P. australis, literature and field surveys for insects and pathogens associated with common reed have been conducted in North America and Europe since 1998 (Schwarzländer & Häfliger, 1999; Tewksbury et al., in prep.). In Europe, at least 151 herbivore species feed

on *P. australis*, some of which cause significant damage; about 50% of these species are considered specialist herbivores of common reed (Schwarzländer & Häfliger, 1999).

Literature (covering all of North America) and field surveys (in the northeastern United States) reveal that at least 26 herbivores attack P. australis in North America (Tewksbury et al., in prep.). Five of these species may be native; the rest are accidental introductions that occurred during the past several decades (Tewksbury et al., in prep.). Two species, the Yuma skipper, Ochlodes yuma, a species distributed throughout the western United States, and a gall midge, Calamomyia phragmites, are considered native and monophagous on P. australis (Gagné, 1989; Tewksbury et al., in prep.). The native broad-winged skipper, Poanes viator, has expanded its diet to include P. australis along the Atlantic Coast as far north as Massachusetts (Opler & Krizek, 1984; Glassberg 1999) and the species is now common in Rhode Island (Tewksbury et al., in prep.). The rhizome-feeding noctuid moth Rhizedra lutosa was first reported from North America in 1988 from New Jersey (McCabe & Schweitzer, 1991). It subsequently was found in the Catskill Mountains of New York in 1991 (Mikkola & Lafontaine, 1994) and by 1999 was recorded from Rhode Island, Connecticut, Massachusetts, and as far west as Ohio (Tewksbury et al., in prep.). The moth Apamea unanimis was first collected in 1991 near Ottawa, Canada (Mikkola & Lafontaine, 1994); larvae feed on leaves of P. australis, Phalaris, and Glyceria. Apamea ophiogramma was first reported in 1989 from British Columbia, Canada (Troubridge et al., 1992) but has since been found in New York, Vermont, Quebec, and New Brunswick (Mikkola & Lafontaine, 1994). Four European shoot flies of the genus Lipara (L. lucens, L. rufitarsis, L. similis, and L. pullitarsis) and the mealybug Chaetococcus phragmitis have been reported from the Northeast (Tewksbury et al., in prep.). Additional species such as the gall midge Lasioptera hungarica, a dolichopodid fly Thrypticus sp., the aphid Hyalopterus pruni and the wasp Tetramesa phragmitis appear widespread. The mite Steneotarsonemus phragmitidis was recently discovered in the Finger Lakes Region of New York and the rice grain gall midge Giraudiella inclusa in Massachusetts, Connecticut, New Jersey, and New York (Blossey & Eichiner, unpubl. data). These are the most commonly recognized species; a complete list of all 26 species recorded on P. australis can be found in Tewksbury et al. (in prep.). It is very likely that more detailed investigations and more extensive field surveys will reveal additional species associated with *P. australis* in North America.

PHRAGMITES AUSTRALIS IN VIRGINIA

The Division of Natural Heritage (DNH) of the Virginia Department of Conservation and Recreation manages a statewide system of Natural Area Preserves (NAPs) dedicated for protection of rare natural communities, species, and their habitats. The DNH is concerned that *P. australis* is expanding in many coastal NAPs. *Phragmites australis* is common in Virginia, especially in the marshes of the Chesapeake Bay and its tributaries, and in the marshes of Back Bay and the Northwest and North Landing rivers in the extreme southeastern corner of the state (Fig. 1).

From 1977 to 1990, a 5-10 fold increase in percent cover of P. australis was documented in Back Bay, City of Virginia Beach (Priest & Dewing, 1991). This expansion is creating monospecific stands, replacing diverse marsh communities and threatening unique and rare communities, including a globally rare (Natural Heritage Network/The Nature Conservancy rank G1G2) community, the Spikerush-Olney Threesquare Marsh (Eleocharis fallax-Eleocharis rostellata-Scirpus americanus-Sagittaria lancifolia tidally flooded marsh), at the Northwest and North Landing rivers, in the cities of Chesapeake and Virginia Beach (Fleming & Moorhead, 1998). Phragmites australis has been ranked A, indicating that it is a species exhibiting "the most invasive tendencies in natural areas and native plant habitats," by DNH and the Virginia Native Plant Society (1999).

Efforts to protect and restore vulnerable biological resources must include control of *P. australis*. DNH led an interagency evaluation (Clark, 1997) of the



Fig. 1. Distribution of *Phragmites australis* by county in Virginia (Harvill et al., 1992).

feasibility of effectively controlling P. australis in southeastern Virginia using a combination of herbicide application and prescribed fire. Stands of P. australis were sprayed with glyphosate in early autumn for two successive years. Large stands were sprayed from helicopter and fixed-wing aircraft, while small stands were treated from the ground using hand-pumped sprayers. Many of these stands were burned between herbicide applications. The degree of control was highly variable, but most stands exhibited an intermediate level of control. Intermediate control was characterized as stands in which much of the P. australis was killed but which contained strips and patches of healthy P. australis and areas of re-sprouts. Such stands will require further monitoring and treatment to prevent subsequent P. australis expansion. The study determined that control of established stands of P. australis is expensive, labor-intensive, and not always successful. However, this treatment methodology is now commonly being used in the mid-Atlantic region as the only means to potentially slow the expansion of P. australis.

Current efforts within DNH involve the use of vegetation plot samples, global positioning systems (GPS), and remotely sensed imagery to map ecological communities of the wetlands of the Northwest, North Landing, and Pamunkey rivers. Delineating stands of *P. australis* provides information on distribution, areal extent, and proximity to sensitive communities to facilitate protection and management of biological resources.

Although *P. australis* is widespread in the coastal areas of Virginia, there have been no records of herbivores associated with this plant from the state. In this paper we report the discovery of four introduced European species in Virginia, known to be specialized on *P. australis*, at two field sites, 49 km (30 mi) apart (Fig. 2). Both sites were visited on 8 March 2000 and surveyed for insect herbivores.



Fig. 2. Field sites visited on 8 March 2000.

FIELD SITES

The first field site was in the town of Tappahannock (Essex County), adjacent to the parking lot of a marina on the southern shore of the Rappahannock River, just west of the U. S. Route 360 bridge. *Phragmites australis* grows in a several-meter wide by approximately 100 m long, relatively dense stand (shoot height 2-4 m) between the parking lot and a shallow bay bordered by a *Spartina patens* marsh. This stand is flooded during periods of high water.

Dameron Marsh NAP, the second site, is located on the western shore of the Chesapeake Bay in Northumberland County. Saltmarsh communities occupy more than half of this 132 ha (316 acre) preserve, with the remaining area consisting of pinehardwood forests, tidal mud flats, beaches, and fallow fields. Common reed grows on the preserve in several separate clones (total area ca. 2 ha) near the high water mark and on a fallow field. Approximate plant height ranged from 1 (fallow field) to 4 m.

METHODS

At each field site, shoots were surveyed for signs of insect attack. Stems showing signs of herbivore feeding or abnormal growth were cut at soil level and dissected at the site to search for internally feeding larvae. Additional random samples were taken and dissected at each site. At the Tappahannock site, approximately 50 randomly selected shoots were collected and dissected on site and 60 additional shoots were taken to Ithaca, New York to confirm species identification and to rear adult specimens. At Dameron Marsh NAP, visual inspection of shoots started with the fallow field followed by the examination of the older, longestablished clones along the shoreline. Several visibly attacked shoots, as well as approximately 50 randomly selected shoots, were dissected on site, and a reference sample of 80 stems was taken to Ithaca to confirm species identification and to rear adults.

RESULTS

Four species (*Lipara rufitarsis*, *Lasioptera hungarica*, *Tetramesa phragmitis*, and *Chaetococcus phragmitis*) not previously recorded from Virginia were identified during this study. All four species are accidental introductions from Europe and not native to North America. An additional Diptera species discovered in the samples as larvae was reared in the laboratory to obtain adults for species identification, but all larvae subsequently died and additional samples will be needed to determine the species. Reference specimens are deposited in the Cornell University Insect collection under Lot # 1241.

Lipara rufitarsis Loew (Diptera, Chloropidae)

The genus *Lipara* Meigen is restricted to the Palaearctic region and all 9 recognized species use *P*. *australis* as their sole host plant (Beschovski, 1984). The four European species *L. lucens*, *L. rufitarsis*, *L. similis*, and *L. pullitarsis* cause more or less distinct apical shoot galls, in which the mature larvae overwinter (Chvala et al., 1974). A single larva develops per shoot (de Bruyn, 1994). All four species are widely distributed throughout Europe with variable but usually low (5-10%) attack rates (Schwarzländer & Häfliger, 1999).

Sabrosky (1958) reported the first North American record of L. lucens in Connecticut on the basis of specimens collected in 1931. He also reported intercepting L. similis in New York in a shipment from the Netherlands where dry P. australis stems were used as packaging materials (Sabrosky, 1958). Use of P. australis as packaging material may be a primary mode of introduction for many other insects that overwinter in dry stems of this species. Recent regional surveys in the Northeast (Tewksbury et al., in prep.; Blossey & Eichiner, unpubl. data) reveal that L. rufitarsis, L. similis, and L. pullitarsis are widespread and abundant. Lipara lucens has not been found in North America since the initial record in 1931, suggesting that the species may not be established on this continent. Taxonomic identification of adult flies is difficult and the species recorded in 1931 may have been misidentified and might actually be L. rufitarsis. Recent attempts to locate the specimens have been unsuccessful (N. Muth, pers. comm). In the Northeast, attack rates of stems, particularly by L. similis, can approach 80% (Blossey & Eichiner, unpubl. data).

The previous southernmost record of *L. rufitarsis* was along the coast of southern New Jersey (Blossey & Eichiner, unpubl. data). The new records from Tappahannock and Dameron Marsh NAP in Virginia extend the distribution of this species several hundred kilometers south. No surveys for *P. australis* herbivores have been conducted south of Dameron Marsh NAP in Virginia, or in other southeastern states. However, the abundance of *L. rufitarsis* at Dameron Marsh NAP suggests that its occurrence in other *P. australis* stands has gone unnoticed.

Larval feeding by L. rufitarsis causes stunting of the 2-4 apical internodes of P. australis and the formation of a cigar-shaped gall at the shoot tip. Infested shoots do not flower, remain much smaller, and, characteristic of all Lipara attacks, show a dry leaf extending from the gall. Galls produced by L. rufitarsis can be distinguished from attack by other Lipara species using criteria of gall morphology and larval overwintering habit. Lipara lucens causes stunting of 10-13 internodes, and larvae penetrate the growing point to feed in a gall chamber. Lipara rufitarsis causes stunting of only 2-4 internodes with larvae also penetrating the growing point. Lipara pullitarsis causes stunting of the apical internodes and gall formation similar to L. rufitarsis but larvae overwinter above the growing point. Lipara similis causes only barely visible alterations of the shoot diameter, but infested shoots can be easily identified by the dried up apical leaves and the lack of an Similar to L. pullitarsis, L. similis inflorescence. larvae feed and overwinter above the growing point of the attacked shoots. Pupation of the larvae occurs in early spring and flies most likely emerge in May. By mid-summer attacked stems should be visible by the dry leaves extending from the shoot tip.

Lasioptera hungarica Möhn (Diptera, Cecidomyiidae)

Lasioptera hungarica is a univoltine gall midge with P. australis as the only recorded host plant (Skuhrava & Skuhravy, 1981). The species appears to be most common in eastern and southern Europe (Schwarzländer & Häfliger, 1999). Infested shoots show no obvious signs of damage; however, they often break in strong winds at the site of attack, suggesting a weakening of the stem tissue. Larvae overwinter in the stem and often 30-300 yellow-orange larvae can be found in a single internode. The species is easily identified by its association with a black fungal mycelium, genus Sporothrix, that fills the internode (Skuhrava & Skuhravy, 1981). Oviposition by females also infects the stem with fungal spores providing food the developing larvae. A parasitic wasp for (identification pending) commonly attacks the species, and birds in certain areas of the Northeast have learned to forage for larvae (Blossey et al., unpubl. data).

Lasioptera hungarica was recognized to occur in North America only in 1999 (Tewksbury et al., in prep.) but the species is widespread throughout the Northeast in Connecticut, Massachusetts, New Jersey, and New York (Blossey & Eichiner, unpubl. data). The records from Tappahannock and Dameron Marsh NAP are the southernmost known occurrences but additional surveys in North America may document a much wider distribution of *L. hungarica*. The range of the species and the limited dispersal ability of adult gall midges indicate a long-term presence of *L. hungarica* in North America.

Tetramesa (Gahaniola) phragmitis Erdös (Hymenoptera, Eurytomidae)

phragmitis Tetramesa is a phytophagous, monophagous wasp with larvae living gregariously (2-12) inside P. australis stems where they also overwinter. Shoots attacked by this wasp show no visible signs of damage and presence of the species is only revealed upon dissections. Larval feeding inside the internodes is very minimal and hard to detect. It can probably be best described as a "scraping" of the interior stem with no impact on shoot growth. Krombein et al. (1979) reported T. phragmitis from America. Recent surveys indicate North that T. phragmitis is the most widespread herbivore of P. australis throughout North America and was also found in samples from California (Blossey & Eichiner, unpubl. data). The species is often attacked by a parasitic wasp (species identification pending) that consumes all larvae. The parasitic wasp can be identified by the presence of a long white cocoon replacing the Tetramesa larvae. Only a single stem was found to be attacked by T. phragmitis at Dameron Marsh NAP. The species was not found at the Tappahannock field site in March 2000, but a recent additional field visit in November 2000 found several stems attacked by T. phragmitis in a P. australis stand across the river (Blossey, pers. obs.).

Chaetococcus phragmitis Marchal (Homoptera, Pseudococcidae)

The legless reed mealybug, *Chaetococcus phragmitis*, has recently been found in Delaware, Maryland, New Jersey, southern New York (Kosztarab, 1996; Krause et al., 1997) and Connecticut (Blossey & Eichiner, unpubl. data), and can be quite abundant (Krause et al., 1997). The only known host plants of this mealybug are *Phragmites* and *Arundo* spp. (Kosztarab, 1996). Although *C. phragmitis* was not reported during recent surveys in Western and Central Europe (Schwarzländer & Häfliger 1999), the species is native to Western and Central Europe, Armenia,

Azerbaijan, and the Mediterranean region (Kosztarab & Kozar, 1988; Ben-Dov, 1994; Hendricks & Kosztarab 1999). In Virginia, it was not found in spring 2000 at Tappahannock but was recorded recently during an additional field visit (Blossey, pers. obs.) and the species was abundant on older clones at Dameron Marsh NAP. The mealybugs feed and overwinter under leaf sheaths and North American birds such as the Black-capped Chickadee (*Poecile atricapilla*) have discovered this abundant food source (Blossey & Eichiner, unpubl. data).

DISCUSSION

Our very limited surveys of P. australis at Tappahannock and Dameron Marsh NAP resulted in the discovery of four species of insect herbivores new to the Virginia fauna. The mealybug and L. rufitarsis are fairly abundant. More extensive surveys at other sites and during the growing season are likely to record additional species. At field sites in New Jersey as many as nine different species were found in similar winter surveys (Blossey & Eichiner, unpubl. data). The regional survey conducted in the Northeast (Blossey & Eichiner, unpubl. data) revealed that the number of accidentally introduced species is highest in close vicinity to New York City, most likely the primary source of new introductions for P. australis herbivores. Currently, many species appear to be spreading and a number of new records can be expected in Virginia within the next few years.

The abundance of accidentally introduced insect herbivores of P. australis in North America requires an evaluation of a potential implementation of a biological control program and a re-assessment of currently employed control techniques. We have very little information about the impact of the accidentally introduced herbivores on this invasive plant in North America. Many of the insects recorded from P. australis have been studied extensively in Europe (Tscharntke 1992a, b) where they are considered pests of reed beds (Mook & van der Toorn, 1982). Generally, these studies lack information on the impact of herbivores on host plant population dynamics, so we are unable to predict their impact in North America. However, the prevalent control methods using herbicides and fire eliminate all herbivores that overwinter as adults, larvae or eggs in P. australis stems. This may, in fact, limit their potential to reduce the spread or decrease the abundance of P. australis in North America. More detailed investigations on the impact of these herbivores on P. australis performance are urgently needed to assess whether a change in management recommendations aimed at preserving populations of these herbivores is needed. Investigations aimed at assessing the impact of these herbivores on native marsh vegetation may also be warranted.

ACKNOWLEDGMENTS

We thank Tom Smith and Steve Carter-Lovejoy for their reviews of the manuscript. We also thank Florian Eichiner for processing most of the stems taken back to the laboratory at Cornell University.

LITERATURE CITED

Ben-Dov, Y. 1994. A Systematic Catalogue of the Mealybugs of the World (Homoptera: Coccoidea: Pseudococcidae and Putoidae) with Data on Geographical Distribution, Host Plants, Biology and Economic Importance. Intercept Ltd. Andover, United Kingdom. 686 pp.

Beschovski, V. L. 1984. A zoogeographic review of Palaearctic genera of Chloropidae (Diptera) in view of origin and formation. Acta Zoologica Bulgarica 24: 3-26.

Besitka, M. A. R. 1996. An ecological and historical study of *Phragmites australis* along the Atlantic Coast. Master's thesis. Drexel University, Philadelphia, PA. 53 pp.

Chambers, R. M. 1997. Porewater chemistry associated with *Phragmites* and *Spartina* in a Connecticut tidal marsh. Wetlands 17: 360-367.

Chvala, M., J. Doskocil, J. H. Mook, & V. Pokorny. 1974. The genus *Lipara* Meigen (Diptera, Chloropidae); systematics, morphology, behaviour, and ecology. Tijdschrift voor Entomologie 117: 1-25.

Clark, K. H. 1997. Southern Watersheds common reed project. Natural Heritage Technical Report 96-19. Virginia Department of Conservation and Recreation, Division of Natural Heritage, Richmond, VA. 35 pp.

De Bruyn, L. 1994. Lifecycle strategies in a guild of dipteran gallformers on the common reed. Pp. 259-281 In M. Williams (ed.), Plant-galls: Organisms, Interactions, Populations. Claredon Press, Oxford, England.

Fleming, G. P., & W. H. Moorhead III. 1998. Comparative wetlands ecology study of the Great Dismal Swamp, Northwest River, and North Landing River in Virginia. Natural Heritage Tech. Report 98-9, Virginia Department of Conservation and Recreation, Division of Natural Heritage, Richmond, VA. 181 pp.

Gagné, R. J. 1989. The Plant-feeding Gall Midges of North America. Cornell University Press, Ithaca, NY. 365 pp.

Glassberg, J. 1999. Butterflies Through Binoculars: The East. A Field Guide to the Butterflies of Eastern North America. Oxford University Press, New York, NY. 242 pp.

Harvill, A. M., Jr., T. R. Bradley, C. E. Stevens, T. F. Wieboldt, D. M. E. Ware, D. W. Ogle, G. W. Ramsey, & G. P. Fleming. 1992. Atlas of the Virginia Flora III. Virginia Botanical Associates, Burkeville, VA. 144 pp.

Haslam, S. M. 1972. Biological flora of the British Isles, no. 128. *Phragmites communis* Trinidad. Journal of Ecology 60: 585-610.

Hendricks, H. J., & M. Kosztarab. 1999. Revision of the Tribe Serrolecaniini (Homoptera Pseudococcidae). Walter de Gruyter, New York, NY. 213 pp.

Kosztarab, M. 1996. Scale Insects of Northeastern North America. Virginia Museum of Natural History, Special Publication Number 3, Martinsville, VA. 650 pp.

Kosztarab, M., & F. Kozar. 1988. Scale Insects of Central Europe. W. Junk Publishers, Boston, MA. 456 pp.

Krause, L. H., C. Riemtsma, & E. Kiviat. 1997. Terrestrial insects associated with *Lythrum salicaria*, *Phragmites australis*, and *Typha angustifolia* in a Hudson River tidal marsh. Pp. V1-V35 *In* W. C. Nieder & J. R. Waldman (eds.), Final Report of the Tibor T. Polgar Fellowship Program, 1996. Hudson River Foundation and New York State Department of Environmental Conservation, New York, NY. Krombein, K. V., P. D. Hurd, D. R. Smith, & B. D. Burks. 1979. Catalog of Hymenoptera in America North of Mexico. Smithsonian Institution Press, Washington, DC. 2,735 pp.

Marks, M., B. Lapin, & J. Randall. 1994. *Phragmites* australis (*P. communis*): Threats, management, and monitoring. Natural Areas Journal 14: 285-294.

McCabe, T. L., & D. F. Schweitzer. 1991. *Rhizedra lutosa* (Lepidoptera: Noctuidae) newly introduced to North America. Entomological News 102: 130-132.

Metzler, K., & R. Rosza. 1987. Additional notes on the tidal wetlands of the Connecticut River. Newsletter of the Connecticut Botanical Society 15: 1-6.

Mikkola, K., & J. D. Lafontaine. 1994. Recent introductions of riparian noctuid moths from the Palaearctic region to North America, with the first report of *Apamea unanimis* (Huebner) (Noctuidae: Amphipyrinae). Journal of the Lepidopterists' Society 48: 121-127.

Mook, J. H., & J. Van der Toorn. 1982. The influence of environmental factors and management on stands of *Phragmites australis* 1. Effects of burning, frost and insect damage on shoot density and shoot size. Journal of Applied Ecology 19: 477-499.

Opler, P. A., & G. O. Krizek. 1984. Butterflies East of the Great Plains: an Illustrated Natural History. Johns Hopkins University Press, Baltimore, MD. 294 pp.

Priest, W. I., III, & S. Dewing. 1991. The marshes of Back Bay, Virginia. Pp. 222-248 *In* H. G. Marshall & M. D. Norman (eds.), Proceedings of the Back Bay Ecological Symposium, Department of Biological Sciences, Old Dominion University, Norfolk, VA. Sabrosky, C. W. 1958. A *Phragmites* gall-maker new to North America (Diptera, Chloropidae). Proceedings of the Entomological Society of Washington 60: 231.

Schwarzländer, M., & P. Häfliger. 1999. Evaluating the potential for biological control of *Phragmites australis* (Cav.) Trin. ex Steudel. Annual report, CABI Bioscience Centre Switzerland, Delémont, Switzerland. 39 pp.

Skuhrava, M., & V. Skuhravy. 1981. Die Gallmücken (Cecidomyiidae, Diptera) des Schilfes (*Phragmites* communis Trin.). Academia Praha, Studie Csav. 3: 1-150.

Troubridge, J. T., S. M. Fitzpatrick, & J. D. Lafontaine. 1992. *Apamea ophiogramma* (Esper), a Palearctic cutworm new to North America (Lepidoptera: Noctuidae). Canadian Entomologist 124: 109-112.

Tscharntke, T. 1992a. Cascade effects among four trophic levels: bird predation on galls affects density-dependent parasitism. Ecology 73: 1689-1698.

Tscharntke, T. 1992b. Fragmentation of *Phragmites* habitats, minimum viable population size, habitat suitability, and local extinction of moths, midges, flies, aphids, and birds. Conservation Biology 6: 530-536.

Tucker, G. C. 1990. The genera of Arundinoidea (Gramineae) in the southeastern United States. Journal of the Arnold Arboretum 71: 14-171.

Virginia Department of Conservation and Recreation and Virginia Native Plant Society. 1999. Invasive alien plant species in Virginia. Richmond, VA.